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TEMPORAL CHANGES IN REEF FISH PREY POPULATIONS AT FRENCH FRIGATE SHOALS, NORTHWESTERN HAWAIIAN ISLANDS: IMPLICATIONS FOR JUVENILE MONK SEAL (*MONACHUS SCHAUINSLANDI*) PREDATORS

EDWARD E. DEMARTINI,
FRANK A. PARRISH
and JAMES D. PARRISH

Honolulu Laboratory
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

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Edward E. DeMartini and Frank A. Parrish

Honolulu Laboratory
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
Honolulu, HI 96822-2396

and

James D. Parrish

Hawaii Cooperative Fishery Research Unit
U.S. Fish and Wildlife Service
University of Hawaii
2538 the Mall
Honolulu, Hawaii 96822

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INTRODUCTION

The Hawaiian monk seal, *Monachus schauinslandi*, is endemic to the Hawaiian Archipelago and is currently distributed among five main breeding populations only in the Northwestern Hawaiian Islands (NWHI). In 1976, this pinniped was designated endangered under the Endangered Species Act of 1973, after a decline in abundance of approximately 50% between the late 1950s and 1970s. The decline occurred at all locations except French Frigate Shoals (FFS), a multi-islet atoll approximately 750 km northwest of the main Hawaiian Islands (MHI). The population at FFS grew extensively during this period and, at present, approximately 40-45% of all Hawaiian monk seals are found at this atoll. However, since 1988, the FFS population has declined by approximately 20-30% (NMFS, unpub. data). The decline is apparent not only in the number of seals observed on the beaches but also in related life history parameters. Between 1989 and 1992, annual survival of pups and juveniles dropped from approximately 0.8 to 0.5 or lower. The number of pups born decreased from a high of 127 in 1988 to 82 in 1991 and then increased to 102 in 1992. Concurrently, birth rate of adult females declined from an expected annual rate of approximately 0.6 to just over 0.3.

The Protected Species Investigation (PSI) is responsible for monitoring Hawaiian monk seal populations and facilitating their recovery. In response to the changes observed at FFS, PSI intensified studies at this site. Initial results indicated that the primary cause of the decline is probably related to lack of available prey, particularly for younger seals. Other possible explanations have either been ruled out (see, for example, a report by Gilmartin and Ragen [1992] on results of disease screening) or are not consistent with the entire set of observed changes and may therefore provide only a partial explanation of those changes.

To further investigate the hypothesis that the observed changes are related to limited prey availability, PSI enlisted personnel from the Insular Resources Investigation (IRI), to conduct a study to determine if a decline has occurred in fish

stocks that are potential prey for seals. Fish stocks were assessed in reef habitats near commonly used haul-out areas in the northwest region of the atoll (Craig et al. 1992).

The feeding habits and foraging microhabitats of monk seals are unknown. Studies of foraging distributions of older animals are being conducted, but the results may or may not pertain to juveniles. Scats and spews are collected opportunistically, but these samples are biased toward nearshore prey with hard tissues that are not dissolved during digestion. Hence, the specific prey of monk seals is not well known, and for this reason, efforts by IRI focused on sampling and estimating densities of higher taxonomic categories of reef fishes at FFS.

METHODS

Sampling

During 1980-83, the densities of shallow-water demersal fishes were estimated at FFS as part of a study of the trophic relationships on these reefs (Parrish et al. 1985; Norris and Parrish 1988). Quantitative, repeated visual diver-surveys were conducted on three trips (May-June and October-November 1980, late March 1983); nine stations were sampled 2-4 times each on at least one of the trips. The two main types of shallow-reef habitats at FFS were sampled with approximately equal effort. Four stations were located in expansive barrier reef habitats, and five patch reef stations were in the lagoon of the atoll (Fig. 1). A total of 43 samples were collected (Appendix Table 1), of which 36 (9 stations x 4 samples·station^{-1}) were chosen based on sampling sequence as representing baseline conditions in barrier reef and patch reef habitats at the atoll.

Another five surveys (of 2 samples each) were conducted at a single, similarly undisturbed patch reef (station 5c) in January, July, October, and November, 1982 and January 1983. Together with 2 samples each in October 1980 and March 1983, a total of seven surveys and 14 samples were available for station 5c. These station 5c data were used to help interpret shorter-term

temporal variation in fish densities within the baseline period.

During July 4-14, 1992, reef fish densities at the same nine stations were estimated using techniques identical to those in 1980-83. Divers visually counted all non-cryptic (mostly day-active) fishes present on belt transects (Brock 1954) or within otherwise delimited areas of reef during daylight (0800-1700) hours. A two-diver team always conducted simultaneous fish counts at a station.

Belt transects of constant dimensions (50 m long x 10 m wide; 500-m^2 area) were surveyed in expansive barrier reef habitats. A 50-m-long line divided the transect area into two contiguous and parallel strips (each 50 m long x 5 m wide). Starting at the same end of the transect, the two-person team (Divers 1 and 2) first swam out along the length of the transect. Divers 1 and 2 proceeded abreast (5 m apart), and each tallied fish encountered within each of five, end-on-end, 10-m-long x 5-m-wide (50-m^2) quadrats, on left (L) and right (R) sides of the line, respectively. The divers then switched sides, reversed direction, and swam back along the length of the transect, so that Diver 2 surveyed the strip just surveyed by Diver 1, and vice versa. In this manner, each diver tallied fishes within the same series of 10, 10-m-long x 5-m-wide quadrats, and each diver's total count represented a single density estimate (number of fish per 500 m^2). Each diver spent approximately 2.5 min surveying each quadrat (total dive duration about 30 min). Fishes were tallied as encountered, by species (or lowest recognizable taxon).

On patch reefs, divers were able to census entire habitats by cordoning reefs into 6 (3L plus 3R), 5-m-long by 5-m-wide, quadrats within a 15-m-long x 10-m-wide (150 m^2) search area that included the fringing sand-rock ecotone. Divers 1 and 2 counted all fishes encountered in a quadrat-by-quadrat search, following the procedure used for transects at the barrier reef stations. Each diver's total count thus represented a single density estimate (number of fish per 150 m^2). Censuses required about

4.5 min per quadrat; therefore, dives lasted about 30 min. As for belt transects at barrier reef stations, a maximum of one pair of censuses was conducted at a patch reef station on a given date.

Quadrat-specific data were not included in our temporal comparisons (see Analyses). Specific sampling protocols, however, importantly influence transect estimates (Sale and Sharp 1983), and it is essential to repeat exact protocols if future surveys are to be quantitatively duplicated. Protocols are therefore provided herein for future reference.

Body size distributions of fishes were characterized using in situ visual length estimates on the summer 1992 surveys. (Visually estimated body length data were not comprehensive on the 1980 and 1983 surveys and are not included in this report.) While two divers were estimating or censusing the numbers of fishes, the third diver estimated the lengths of all fishes encountered on a haphazard, 30-min swim throughout the general station area (while avoiding the other two divers). Post-recruit-stage ($\geq$1-in standard length, SL) fish encountered within 1 to 3 m of the diver were tallied by length class. Length-classes were progressively broader for larger fish, as follows: 1-2 in, 2-3 in, 3-4 in, 4-5 in, 5-6 in, 6-7 in, 7-10 in, 10-15 in, 15-20 in, 20-30 in, 30-40 in, 40-50 in, >50 in.

Prior to the cruise, the three divers practiced visual length estimates of free-swimming fish underwater. They then estimated the lengths of 35 moving (tethered), fresh-dead fish specimens during a pre-cruise test session. Estimates of mean body lengths were indistinguishable among the three personnel and the actual fish lengths (ANOVA; $F_{3,136} = 2.3$; $P = 0.1$). Divers' estimates were $\pm$ 9-11% of actual lengths. Specimens of the commoner reef species, with body length distributions similar to those of the fishes at FFS, were used for training and testing.

The three members of the dive team were rotated between the density and length estimation tasks to randomize diver effects among stations. Such precautions minimized potential biases

(inaccuracy) at the expense of some loss in precision (DeMartini et al. 1989).

Analyses

Fish assemblage structure was evaluated in terms of the relative commonness and relative abundance of species. Commonness was evaluated as frequency of occurrence (i.e., the number of transects on which a species occurred) and abundance by density on transects. Spearman's rank-order correlation (Siegel and Castellan 1988) was used to test for similarity of assemblages between habitat types and sampling periods.

Matched-pairs designs were used for primary analysis of temporal patterns in density, with the data matched by sampling station and paired by the time period (Before: 1980-83; After: 1992) in which samples were collected. Both parametric (paired *t*-test) and nonparametric (matched-pairs signed-ranks test) procedures were used. The basic datum analyzed was the (rank) best-estimated density (per $10m^2$; Norris and Parrish 1988) for each sampling location and time period; a constant four, repeat counts were averaged and this mean used to represent the basic datum. For paired *t*-tests, the criterion variable was the delta (before minus after period difference) of the station-specific estimate. The nonparametric analogue of this variable was the signed-rank of the station-period difference (Siegel and Castellan 1988). Thus, sample size and statistical power were determined by the number of stations sampled (nine), rather than the total number of samples or transects. In cases where deltas were especially skewed, station means were transformed to common logarithms ($\log_{10}$ [x+1]) to normalize distributions prior to derivation of deltas and calculation of paired *t*-tests.

Simple *t*-tests also were calculated and the results compared with those of the paired *t*-tests to evaluate the potential improvement that pairing by station had on the temporal comparisons. Log_{10} (x+1) station means were used as criterion variables, and Satterthwaite's approximation (Bailey 1981) was

used to reduce degrees of freedom appropriately if variances remained heterogeneous following transformation. Standard errors of the station means also were used to estimate spatial variation in abundance among stations within each of the two sampling periods.

Statistical analyses used the procedures PROC MEANS, RANK, CORR, TTEST, and GLM of the Statistical Analysis System (SAS 1985). Siegel and Castellan (1988) was consulted for binomial tests. Two-tailed probabilities ($\alpha_2 = 0.05$) were used except when a one-tailed test ($\alpha_1 = 0.05$) of a specific prediction was more appropriate. Bonferroni's inequality (Harris 1985, p.7) was used to adjust probability values for n multiple comparisons ($\text{alpha}_{crit} \leq \text{alpha}_{.05}/n$) as necessary.

Statistical power (Cohen 1988) was evaluated using the deltas of major taxa and taxonomic groupings of fishes, and the sample sizes required for detecting changes of defined magnitude were thereby estimated. Sample size estimates assumed that distributions of the deltas (based on either the raw or the log-transformed means, depending on which was less skewed) approximated normality.

Analyses focused on potential temporal patterns for total reef fishes in both habitat types because of the uncertainties regarding the specific diet and foraging microhabitats of monk seals. In addition, we explored whether temporal changes were detectable for either of the two major trophic levels (primary consumers or herbivores, secondary consumers or carnivores) that comprise total fishes. We further evaluated each of four foraging guilds included within the carnivore level (benthic invertebrate-feeders, hereafter referred to as benthic carnivores; zooplanktivores; corallivores; and piscivores). Recorded taxa were classified into trophic levels and foraging guilds using Hobson (1974), Randall (1985), and Norris and Parrish (1988). Omnivores were assigned entirely to one or the other trophic level based on whether animal or plant matter dominated the diet; analogous decisions were made for carnivore

guilds. Counts of taxa were summed within levels and guilds prior to analyses.

For the summer 1992 data only, length frequency tallies were converted to biomass using the weights of mid-point length classes estimated from specific length-weight regression parameters (J. D. Parrish, unpubl. data). Estimated weights were summed over all taxa for total fishes and summed separately for component herbivores and carnivores.

RESULTS

Assemblage Structure

Tables 1 and 2 characterize the commonness and abundance of major fishes at FFS during the two sampling periods. Table 1 lists the top 30 most frequently encountered fishes on baseline surveys (ranked by the number of full transects on which they occurred); relative frequency occurrence of these same fishes in summer 1992 is also noted. Table 2 similarly lists the top 30 most abundant fishes on baseline surveys (ranked by numerical density). Rankings were correlated between barrier and patch reef habitats in summer 1992 (Spearman's rank-order correlation; occurrence: $r_s = 0.45$; $0.02>P>0.01$; density: $r_s = 0.41$; $0.05>P>0.02$). Rank densities also were correlated for baseline barrier and patch reef data ($r_s = 0.61$; $P<0.001$). For this reason (and because distributional shifts between the two habitats were indicated for some taxa--see "Densities"), data for the two habitats were pooled within sampling period for further analysis of assemblage structure.

Pooled over the two habitats, rankings were significantly concordant between sampling periods for occurrence data ($r_s = 0.60$; $P<0.001$; Table 1) and for density data ($r_s = 0.54$; $0.01>P>0.001$; Table 2). In general the relative abundances, hence taxonomic composition, of FFS reef fishes differed little between the two sampling periods.

A few minor components of the fish fauna nonetheless differed between the two data series. Notable among these was

the conspicuous absence on the summer 1992 survey of two corallivores (the butterflyfish, *Chaetodon unimaculatus* and the blenny, *Exallias brevis*), and the marked decline of another corallivore (fantail filefish, *Pervagor spilosoma*). Two taxa of nocturnal zooplanktivores (cardinalfishes, *Apogon* spp; and bigeyes or "aweoweo," *Priacanthus* spp) were either absent or extremely rare in summer 1992. Altogether, 11 taxa of conspicuous, easily recognizable reef fishes were present on baseline surveys but absent from summer 1992 samples, compared to 7 taxa present in 1992 but absent from the baseline samples (Table 3). These and other specific cases contributing to patterns of temporal change in fish densities are treated in greater detail below.

Despite the general temporal consistencies, many conspicuous and persistent differences existed between the barrier and patch reef fish faunas. One labrid (a benthic carnivore), *Thalassoma ballieui*, was relatively common and abundant at barrier reef, compared to patch reef stations. Another small carnivore, the arceye hawkfish (*Paracirrhites arcatus*) occurred only at barrier reef stations throughout the study. Two corallivores (the damselfish *Plectroglyphidodon johnstonianus* and the butterflyfish *Chaetodon multicinctus*) were more common on the barrier reef. Among zooplanktivores, the damselfish, *Chromis vanderbilti*, was absent from patch reefs, despite consistently high (ranks 1 and 6) densities at barrier reef stations. Herbivores, especially surgeonfishes of the family Acanthuridae, were among the best representated fishes on the barrier reef; many species including *Acanthurus olivaceus*, *A. nigroris*, *A. blochii* (*mata*), and *A. nigrofuscus*, and larger-bodied surgeonfishes collectively (see "Summer 1992 Biomass") were consistently better represented on the barrier reef.

Other species were common or abundant on patch reefs but rare or absent at barrier reef stations. Included among these were several nocturnal, benthic carnivores (the scorpaenid *Dendrochirus barberi* and the holocentrid *Neoniphon* [*Flammeo*]

sammara), the aforementioned *Priacanthus* spp, and diurnally piscivorous lizardfishes (family Synodontidae).

Overall, similarities dominated differences in assemblage structure both spatially (in barrier and patch reef habitats) and temporally (between sampling periods). For completeness, all taxa encountered at the FFS stations during the two survey periods are listed in Appendix Table 2.

Densities

Estimates of the numbers of fish individuals per standard ($10m^2$) area are listed for each of the "Top 20" taxa on baseline transects (all stations pooled; Table 4). Table 4 also lists the densities of each taxon in summer 1992 and its habitat-specific density during each sampling period. These top 20 taxa accounted for 82-96% of the total fish counts on transects, depending on habitat and period (Table 4).

Matched-pair comparisons indicated significant ($\alpha_{crit}=\alpha_{.05}/30$ <0.002) temporal changes for only 4 of 30 taxa (Table 5); each of these four taxa declined 75- to 100-fold. A suggestion of pattern emerges if the sign (direction) of nominal changes is evaluated for the 30 taxa: decreases outnumbered increases (20 versus 10; P = 0.05; binomial test; Table 5). In general, however, species-level data provide relatively little resolution (see Discussion on "Power of Temporal Comparisons").

Patterns of temporal change are obscured when heterogeneous taxa are combined (e.g., total fishes; Fig. 2). Summary data suggest that the total fishes taxon contains varied elements. Herbivores contributed about one-third, and carnivores about two-thirds, to total fish counts in the two habitats during the baseline period. Analogous estimates for summer 1992, however, were about 10% greater and 10% less for herbivores and carnivores, respectively (Fig. 2).

Temporal patterns emerge if taxa are pooled into finer, functional categories. Density changes were detectable for one trophic level and some carnivore guilds. By matched-pair *t*-test,

a nominal 27% decrease in benthic carnivores throughout both habitats was marginally significant at P = 0.04 (if alpha-level is unadjusted for the multiple comparison; Table 6). An apparent decrease of equal magnitude for total carnivores was similarly borderline (P ≈ 0.05 if unadjusted; Table 6; Fig. 2). A much larger (70%) decrease in corallivore density was significant at P<0.01 (Table 6; Fig. 2). In general, the carnivore declines were broad scale--an apparent 47% on the barrier reef and 20% on patch reefs. Nonparametric (matched-pair signed-ranks) tests produced qualitatively similar results for these same pooled taxa (Table 7), which suggests that the parametric paired *t*-tests were not compromised by the normality assumption.

Herbivore densities showed trivial net change if the data for barrier and patch reef stations are pooled (Table 6; Fig. 2). However, pooling obscures a suggestive increase (38%; P = 0.13) in herbivore density on patch reefs, coupled with a complementary decrease (50%; P = 0.01) in herbivore density in barrier reef habitat (Fig. 3). Herbivore changes primarily reflected those of surgeonfishes and among the latter, particularly those of "browsing" micrograzers (Jones 1968) of filamentous algae such as the yellow tang, *Zebrasoma flavescens*. The latter species increased on patch reefs by >1000% (Fig. 3).

Patch Reef Station 5c.

The densities of most pooled taxa at this station varied appreciably among surveys during 1980-83 (Figs. 4A-C). Some taxa (e.g., planktivores; Fig. 4B) varied more during 1980-83 than between these early surveys and the summer 1992 survey. The densities of other taxa, however, changed more at station 5c between 1980-83 and during summer 1992 than they varied during 1980-83 (benthic carnivores; Fig. 4B).

Summer 1992 Size Composition and Biomass

Figure 5 illustrates the size composition of fishes at the two FFS reef habitats in summer 1992; data are presented

separately for primary consumers (herbivores) and secondary consumers (carnivores) in panels A and B, respectively. The length frequency distribution of herbivores was skewed considerably larger at barrier, compared to patch reef, stations (Fig. 5A). The length distribution of carnivores (Fig. 5B) was comparable in the two habitats, with modes at 7-11 cm SL, similar to the length distribution of herbivores on patch reefs (Fig. 5A).

The length composition of carnivores is further partitioned into trophic guilds in Fig. 5B. In both barrier and patch reef habitats, zooplanktivores dominated the smaller size classes ($\leq$7-11 SL), and benthic carnivores were better represented at larger body sizes (Fig. 5B). Corallivores and piscivores, both relatively minor components, were represented at body sizes below and above the 7-11 cm SL mode, respectively (Fig. 5B).

Fish biomass density on the shallow coral reefs of FFS in summer 1992 averaged about 1.0-1.7 $kg \cdot 10m^{-2}$ (at 12.1 $fish \cdot 10m^{-2}$ weighing a mean 80-140 g each). For both FFS habitat types pooled, herbivores contributed a little less than one-half, and carnivores slightly more than one-half, to total fish biomass (Fig. 6).

Biomass density was almost twice as high on patch reefs (>1.1 $kg \cdot 10m^{-2}$) as on the barrier reef (0.6 $kg \cdot 10m^{-2}$). Contribution by trophic level moreover differed between barrier and patch reef habitats, with herbivores dominating biomass (52%) on the barrier reef and carnivores contributing more to fish biomass on patch reefs (57%; Fig. 6).

DISCUSSION

Assemblage Structure

The basic structure of the fish assemblages on shallow FFS reefs was similar for the two habitat types and the two sampling periods. Not surprisingly (Sale 1980, 1989), the data suggest greater differences in composition and relative abundance between

the fish faunas of barrier and patch reefs than between the samples from one habitat type taken at different times.

Temporal persistence in the assemblage structure of fishes has been observed in studies of other coral reef systems, but exceptions also have been reported (reviewed by Sale 1989). Our general understanding of the assemblage dynamics of reef fishes is too meager to speculate on whether changes might be expected between series of samples a decade apart on the same reefs.

Temporal Comparisons of Densities

The after changes in density of some, but not all, higher-level groupings of fishes at FFS likely reflect the confounding of abundances with the distributions of some taxa. Estimates of changes in density of herbivorous fishes were confounded by strong shifts in the spatial distributions of many (primarily surgeonfish) taxa between barrier and patch reef habitats. Density declines for carnivorous fishes, including some major component feeding guilds, were not confounded by distributional shifts. The declines in the densities of carnivorous fishes that we observed in both barrier and patch reefs probably represent decreases in abundance as well as density.

The observed lack of change in overall herbivore densities clearly reflects a net increase at patch reefs canceling a net decrease at barrier reef stations. Contrary to the present biased view of coral reef fishes as semi-sessile organisms (based on studies of small-bodied, shelter-restricted species), larger-bodied surgeonfishes (F. Acanthuridae) and parrotfishes (F. Scaridae) are now known to travel extensively between discrete reef habitats (Robertson 1988). Some species routinely migrate over distances of several kilometers between daytime feeding and nighttime sheltering sites (Bardach 1958; Walsh 1984). Herbivorous reef fishes also have been reported to immigrate to reefs at which algal blooms have resulted from catastrophic declines in urchin grazers (Robertson 1991). Herbivores and other large-bodied, wide-ranging coral reef fishes probably track

food resource distributions that have cascading effects up the trophic system, as vertebrates in many other systems (Hunter et al. 1992). The patterns of between-habitat differences that we observed at FFS for herbivorous fishes in general, and surgeonfishes in particular, are representative of shallow coral reef systems (Bouchon-Navaro and Harmelin-Vivien 1981).

Information from several sources suggests that the observed shifts in the spatial distributions of herbivores at FFS are due to changes in algal resource distributions. Anecdotal, semi-quantitative data (Appendix Table 3) and other information (Atkinson and Grigg 1984) indicate that standing stocks of *Microdictyon* sp (a green alga that is an important food of grazing surgeonfishes; Randall 1961, Jones 1968) were markedly elevated on FFS patch reefs during July 1992, compared to a comparable time in the seasonal cycle within the baseline period (August 1981; R. Grigg, Univ. Hawaii, pers. comm.). Conditions for algal growth on shallow FFS reefs should be similar in July and August. Algae might have increased at FFS in recent years as a result of more frequent and intense storm disturbances clearing additional coral substrata for algal colonization, particularly on shallower patch reefs more subject to physical disturbance.

The decreases in carnivorous reef fishes we observed at FFS might have been influenced by inter-decadal changes in ecosystem productivity in the central Pacific, north of the Hawaiian Islands (Polovina and Mitchum, in prep.). During the period from about 1977 to 1988, many persistent storm events generated unusually turbulent conditions that increased nutrient availability within the photic zone of near-Hawaii waters and might have stimulated primary productivity. This increase could have led to higher productivities of lobster, seabirds and monk seal at FFS during the eighties (Polovina and Mitchum, in prep.). The declines observed at FFS after 1988 may be viewed as returns to more normal, lower levels of productivity (Polovina and Mitchum, in prep.). The recent apparent declines in reef fishes thus may reflect a more typical level of fish abundance, when the

carrying capacity for predators of shallow-reef fishes at FFS is lower. Some of the changes in reef fish numbers at FFS probably represent lagged numerical responses to fluctuations in recruitment resulting from altered levels of planktonic productivity. It should not be surprising then that the observed declines in reef fish stocks were less extreme than the halvings in year-class success of seabirds and monk seals because transect counts include resident fish of a range of ages, and age structure buffers the numerical response of populations to fluctuations in individual year classes.

We emphasize that changes were detectable only for carnivore guilds of FFS reef fishes because possible changes in herbivore abundance would have been obscured by shifts in spatial distributions. Abundance, not density, data would have been needed to evaluate whether herbivorous fish populations have changed at FFS. Lack of data on extent of the two types of reef habitat at FFS unfortunately prevents conversion of herbivore densities to abundances.

Within-Baseline Temporal Variation

The limited data available indicate that fish numbers varied considerably at patch reef station 5c for some pooled taxa, but not for others, on a subannual basis during the period 1980-83. These data suggest the possibility that some fish populations at FSS were already declining (perhaps with the onset of the 1982-83 El Niño) within our baseline period. Pooled 1980-83 data might then represent a heterogeneous baseline that is internally more variable than the mean difference between before and after sampling periods. Greater within- than between-variations preclude analysis of larger-scale temporal (Morrissey et al. 1992) as well as spatial (Underwood 1981, 1991, 1992) patterns.

The data for station 5c alone cannot be used to infer general patterns of short-term variation, however. As a single station in only one of the two habitats, the 5c data may be unrepresentative. For example, the numbers and distributions of

fishes might be confounded among patch reefs or between reef habitats, so that fish abundance did not vary with fish density during 1980-83 throughout the FFS barrier and patch reef system.

Few data exist on within- or among-year variations in fish populations on shallow Hawaiian reefs that could be used to interpret the temporal patterns observed at FFS. One potentially useful data series is that of Schroeder (1989). During a 51-month period from May 1981 to August 1985, Schroeder (1989) censused the abundances of recruit and resident fishes on patch reefs within the lagoon of Midway Atoll, located 700 nmi northwest of FFS in the NWHI. At approximately quarter-year intervals, a total of 19-21 censuses were conducted at each of four control (unmanipulated) patch reefs ranging in size from 10 to 150 m^2. Total counts (recruits plus residents of all species pooled) generally fluctuated less than one-third within reefs, except during brief but large (2- to 4-fold) summertime recruitment spikes (Schroeder 1989, Fig. 5.8). Temporal patterns at Midway, located near the northern limit of coral reefs in the Hawaiian Archipelago, may not adequately reflect the dynamics of fish abundance at FFS, however.

Dr. E. Hobson (unpubl. data; DeMartini et al., in prep.) has conducted annual (September-October) surveys of the fishes at 1-2 stations on several fringing reefs on the Kona (leeward) coast of the island of Hawaii in the MHI, about 600 nmi southeast of FFS. Fishes have been surveyed using fixed, 50-m^2 belt transects in 13 years during the period 1978-92, inclusive. The total numbers of fishes and the numbers of many higher fish taxa have varied little between successive years in the time series; in fact, annual estimates of the densities of many taxa are serially correlated (DeMartini et al., in prep.). Even so, the densities of many taxa have trended upwards at Kona in recent years. We again caution that, as for the fishes at Midway, the abundance dynamics of Kona coast fishes may not represent those of FFS fishes.

In summary, neither our data for patch reef station 5c nor data for elsewhere in the Hawaiian Archipelago (Schroeder 1989; Hobson, unpubl. data, DeMartini et al., in prep.) resolve the issue of whether the differences we observed at FFS during summer 1992 exceed those due to subannual and interannual variability within a period of oceanographic stability.

Power of Temporal Comparisons

Statistical power is defined as one minus the Type II error (i.e., the complement of the probability of failing to reject a false null hypothesis). Power is a design factor that is just as important as the Type I error (alpha level), the latter more commonly explicit with statistical testing (Cohen 1988; Peterman 1990). The power of tests for changes in organism abundance, however, is often poor because it is commonplace for abundances to vary greatly both spatially and temporally and for sample replication to be insufficient because of limitations of time or human resources. Natural variability combined with large sampling error often result in data distributions that overwhelm the ability to discern real changes in central tendency.

The distribution and abundance patterns of reef fishes are no exception (Sale 1991), yet few studies have explicitly acknowledged statistical power when designing surveys and analyzing data on coral reef fish abundances (e.g., Thresher and Gunn 1986). The before versus after data of this report provide an excellent opportunity to present an example of such important information.

In general, the FFS data are either encouraging or discouraging, depending on the taxonomic resolution that is required. Clearly, sampling efforts similar to those conducted are inadequate for detecting less than huge (>100%) increases or catastrophic (>90%) declines for individual fish species. Impractically large sample sizes would be required to detect declines of reasonably large (say 50%; Skalski and McKenzie 1982) magnitude for individual species. Detecting $\geq$50% declines for 9

of the top 10 most common and abundant species listed in Table 4 would require 30-190 samples (where each sample is a station, sampled before and after with four repeat counts), depending on species. Only the saddleback wrasse, *Thalassoma duperrey*, Hawaii's most common and abundant shallow-reef fish (Hourigan and Reese 1987), would likely (at power ≥ 0.80) require <15 samples (14 at $\alpha_2 = 0.05$; 11 at $\alpha_2 = 0.10$).

Power to detect $\geq$50% declines in higher order taxa, however, is acceptable (≥ 0.80) at practical sample sizes (12-15 samples) for total fishes, pooled carnivores, and for some carnivore guilds (Table 8). If the question is answerable at higher taxonomic levels or other larger groupings (as in the present case for the fish prey of monk seals), then using visual diver surveys to estimate reef fish densities is a reasonable undertaking. On the other hand, if species-level discrimination is required, much greater sampling effort would be required.

Our data further illustrate the (perhaps obvious) fact that matched-pair sampling and analysis designs can appreciably improve statistical power to detect changes. This primarily reflects the reduced skew of the deltas (differences) used in paired-difference tests for which data are matched by station, compared to the greater skew of the unmatched station data for each sampling period. The contrasting results of simple *t*-tests versus matched-pair *t*-tests illustrate this point: Standard errors of period means for major pooled taxa were generally 15-30% of the respective mean estimate (Table 6; Fig. 2). With the exception of corallivores, simple *t*-tests were unable to detect any before-after changes in period means. (Excluding corallivores, the two smallest P-values observed were 0.20 for secondary consumers and 0.13 for benthic carnivores.) The standard errors of the corresponding delta-bars (means of the matched-pair deltas), however, were consistently less than the standard errors of either period mean. And declines of one-fourth to one-third were detectable for several major pooled taxa, as previously described.

Summer 1992 Biomass

Total fish numbers at FFS in summer 1992 were nominally 16% lower than during 1980-83 (Fig. 2). Based on fish count (numbers) data, the before-after comparisons indicate that the standing stocks of fishes at FFS were relatively low in summer 1992. Assuming equivalent body size distributions in 1980-83 and in 1992, our 1992 estimates of the mean standing stock biomass of fishes on shallow FFS reefs are nonetheless almost 2-fold *higher* than present average values for fishes on shallow reefs in the MHI (400-600 $g \cdot 10m^{-2}$; R. Brock, Hawaii Inst. Mar. Biol., pers. comm., Sept. 1992).

Although diver counts are more likely to under- than overestimate fish abundances (Sale and Douglas 1981), the consistently narrow transect widths used throughout our study probably minimized the degree of underestimation (Sale and Sharp 1983). We consider it unlikely that the apparent difference between FFS and the MHI is an artifact of different sampling methods because MHI researchers use similarly short and narrow transects. Rather, the difference may reflect the present heavily exploited condition of fish populations on shallow reefs in the MHI. This topic deserves further study.

We believe that our summer 1992 biomass density data are reasonable estimates of absolute values that can be used for subsequent quantitative comparisons of the diurnal, non-cryptic fishes on shallow Hawaiian reefs. In the future, any real differences between the MHI and the NWHI could contribute important information to be used in the development of management plans for shallow-reef resources in the MHI.

SUMMARY AND CONCLUSIONS

The abundances of fishes on shallow (<10-fm) coral reefs at FFS were sampled by trained divers using identical visual-survey techniques during two time periods about a decade apart. Baseline or before period surveys (defined after-the-fact) were conducted in May and October 1980 and in March 1983. An after

survey was completed in summer 1992. Numerical density estimates were compared between the two periods using a matched-pair design where samples were matched by station.

Each of a series of nine stations was sampled with equal effort (four repeat counts) during each period. Approximately equal effort was distributed across the two primary, shallow-reef habitat types at FFS. Four stations were located in expansive habitat on seaward and leeward barrier reefs; five stations were isolated patch reefs within the lagoon of the atoll. All stations were located near areas frequented by monk seals (Tern, Trig, and Whale-Skate Islands) in the northwest portion of the atoll.

Our analyses produced the following major results:

- Fish assemblages differed little between the two sampling periods in terms of the relative commonness and abundance of species. Overall, similarities dominated differences in assemblage structure both spatially and temporally.
- Matched-pair comparisons indicated significant changes for only 4 of 30 taxa, but species-level differences were difficult to evaluate because of low statistical power.
- A suggestion of pattern emerges if the sign of nominal changes in densities is evaluated; apparent decreases tended to outnumber increases at the species level.
- Available data provide sufficient statistical power to meaningfully evaluate major pooled taxa (trophic levels, feeding guilds) of fishes.
- Patterns of temporal change are obscured when heterogeneous taxa are combined, but patterns are apparent when functional categories are used. An example of the former are herbivores, whose temporal patterns of abundance were confounded with distributional shifts between barrier and patch reef habitats. Several carnivore guilds provide examples of the latter.
- In general, our temporal comparison of fish densities is consistent with, but in itself does not provide conclusive proof

that, the abundance of the fish prey of monk seals has declined to a biologically meaningful extent at FFS. Further, it is unknown to what extent the day-active fishes on shallow reefs contribute to the diet of monk seals, especially juveniles. Obviously, our observations have less relevance if night-active fishes (e.g., apogonids, holocentrids), octopus, or lobster dominate the diet of juvenile seals.

■ Summer 1992 size-composition data allowed us to estimate the current biomass densities of fishes on shallow FFS reefs. These estimates seem almost 2-fold higher than typical values for shallow coral reefs in the MHI. This difference may reflect the present highly exploited state of MHI reef fish populations, relative to reef fish populations on pristine reefs of the NWHI, but this speculation requires further study.

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Table 1.--Relative (rank) frequency occurrence (transect basis) for the Top 30 fish taxa encountered at French Frigate Shoals, Northwestern Hawaiian Islands, on 1980 and 1983 baseline surveys (43 transects). Also listed are the analogous rankings of these 30 taxa on the summer 1992 survey (36 transects). Data are for barrier and patch reef stations pooled.

Taxon	(Rank) frequency occurrence (Number of transects)			
	Baseline		Summer 1992	
Thalassoma duperrey	43	1	36	1.5
Stethojulis balteata	41	2.5	28	11
Chaetodon miliaris	41	2.5	25	14
Ctenochaetus strigosus	39	4	34	4
Centropyge potteri	38	5	33	5.5
scarid juveniles	37	6	30	8.5
Labroides phthirophagus	36	7	24	15
Mulloidichthys vanicolensis	35	8.5	6	26.5
Stegastes fasciolatus	35	8.5	36	1.5
Chromis ovalis	33	10	6	26.5
Canthigaster jactator	32	11.5	35	3
Acanthurus triostegus	32	11.5	31	7
Chaetodon fremblii	31	13	28	11
Neoniphon sammara	30	14	17	17.5
Parupeneus multifasciatus	29	16	33	5.5
Bodianus bilunulatus	29	16	28	11
Cheilinus unifasciatus	29	16	14	20.5
Dascyllus albisella	28	19	26	13
Scarus perspicillatus	28	19	17	17.5
Zanclus cornutus	28	19	12	23.5
Chaetodon multicinctus	26	22.5	14	20.5
Chromis hanui	26	22.5	16	19
Scarus sordidus	26	22.5	7	25
Naso unicornis	26	22.5	13	22
Gomphosus varius	25	25.5	20	16
Priacanthus spp	25	25.5	1	29
Macropharyngodon geoffroy	24	27.5	12	23.5
Pervagor spilosoma	24	27.5	2	28
Thalassoma ballieui	23	29	30	8.5
Apogon spp	22	30	0	30

Table 2.--Relative (rank) abundance (numerical density, $N \cdot 10m^{-2}$) for the Top 30 fish taxa encountered at French Frigate Shoals, Northwestern Hawaiian Islands, on 1980 and 1983 baseline surveys. Also listed are the analogous rankings of these 30 taxa on the summer 1992 survey. Density data are the unweighted grand means of barrier and patch reef station means.

	(Rank) numerical density ($N \cdot 10m^{-2}$)			
Taxon	Baseline		Summer 1992	
Thalassoma duperrey	1.98	1	1.36	1
Chromis ovalis	1.33	2	0.11	19
Mulloidichthys vanicolensis	1.29	3	0.22	12
Ctenochaetus strigosus	1.10	4	1.16	3
Dascyllus albisella	0.92	5	1.15	4
scarid juveniles	0.90	6	1.18	2
Stegastes fasciolatus	0.79	7	1.05	5
Chaetodon miliaris	0.56	8	0.98	6
Scarus sordidus	0.52	9	0.05	23
Priacanthus spp	0.48	10	<0.01	29
Neoniphon sammara	0.31	11	0.30	10
Stethojulis balteata	0.29	12	0.16	15
Acanthurus triostegus	0.28	13	0 56	8
Centropyge potteri	0.27	14	0.23	11
Labroides phthirophagus	0.21	15	0.20	14
Canthigaster jactator	0.20	16	0.22	13
Chromis hanui	0.19	17	0.15	17
Chromis vanderbilti	0.16	18	0.63	7
Pervagor spilosoma	0.15	19	<0.01	28
Acanthurus nigroris	0.12	20	<0.01	27
Apogon spp	0.11	21	0.0	30
Scarus perspicillatus	0.10	22	0.06	22
Chaetodon multicinctus	<0.10	23	0.04	24
Naso unicornis	>0.09	24	<0.04	26
Chaetodon fremblii	>0.09	25	0.09	20
Macropharyngodon geoffroy	0.09	26	<0.04	25
Cheilinus unifasciatus	<0.09	27	0.09	21
Mulloidichthys flavolineatus	<0.09	28	0.42	9
Parupeneus multifasciatus	<0.09	29	0.15	16
Bodianus bilunulatus	0.08	30	0.11	18

Table 3.--Listing and comparison of taxa "present in baseline but absent in summer 1992" (P→A) and "absent in baseline but present in 1992" (A→P) diver-observation surveys at French Frigate Shoals, Northwestern Hawaiian Islands. Listing is restricted to readily identifiable reef fishes that would have been recognized and recorded if encountered. See Appendix Table 2 for expanded listing and Table 4 caption for feeding guild abbreviations. Also summarized is the result of the binomial test, evaluating the relative number of P→As and A→Ps.

	P→A	A→P
Aprion virescens(PISC)		x
Cheilinus bimaculatus(BC)	x	
Cirrhitus pinnulatus(BC)	x	
Pterois sphex(BC)		x
Sebastapistes ballieui(BC)	x	
Cheilodactylus vittatus(BC)		x
Lactoria fornasini(BC)	x	
Cantherhines sp(BC)		x
Chaetodon trifascialis(CO)		x
Chaetodon unimaculatus(CO)	x	
Chaetodon lunula(BC)	x	
Exallias brevis(CO)	x	
Chromis verater(PL)	x	
Acanthurus blochii(**HERB**)		x
Acanthurus xanthopterus(**HERB**)		x
Acanthurus dussumieri(**HERB**)	x	
Diodon holocanthus(BC)	x	
Arothron meleagris(CO)	x	
Totals	11	7

H_o : P→A = A→P
H_a : P→A > A→P

11 P→A to 7 A→P; P=0.24 (binomial test)

Table 4.--Baseline (1980, 1983) and summer 1992 numerical densities, D, of reef fishes ($N \cdot 10m^{-2}$) at French Frigate Shoals, Northwestern Hawaiian Islands. The "Top 20" fish taxa are ranked in descending order of their unweighted grand means for the two ('BR' = Barrier, 'PR' = Patch) reef types in the baseline period. Analogous estimates are listed and ranked for summer 1992 samples. Estimates are also provided for each reef type in each period. Primary consumers (Herbivores = HERB) are noted in **bold** type; Secondary Consumers (Corallivores [CO], other Benthic Carnivores [BC], Zooplanktivores [PL], and Piscivores [PISC]) are noted in plain type. An "abs" indicates absence from surveys. The dashed horizontal line separates the "Top 20" from lower-ranked species on baseline period transects.

	Mean density ($N \cdot 10m^{-2}$)							
	Baseline				Summer 1992			
Taxon	$Rank_B$	D_{BR}	D_{PR}	D_{both}	$Rank_A$	D_{BR}	D_{PR}	D_{both}
Thalassoma duperrey(BC)	1	2.11	1.87	1.98	1	.90	1.72	1.35
Chromis ovalis(PL)	2	.36	2.12	1.33	21	.03	.17	.11
Mulloidichthys vanicolensis(BC)	3	.48	1.93	1.29	13	abs	.45	.22
Ctenochaetus strigosus(HERB)	**4**	**1.16**	**1.06**	**1.10**	**3**	**.33**	**1.82**	**1.16**
Dascyllus albisella(PL)	5	.24	1.47	.92	4	.06	2.02	1.15
Scarid juveniles(HERB)	**6**	**.62**	**1.12**	**.90**	**2**	**.19**	**1.98**	**1.18**
Stegastes fasciolatus(HERB)	**7**	**.25**	**1.22**	**.79**	**5**	**.22**	**1.72**	**1.05**
Chaetodon miliaris(PL)	8	.20	.86	.56	6	.03	1.74	.98
Scarus sordidus(HERB)	**9**	**.08**	**.87**	**.52**	**as scarid juvs**			

Table 4.--Continued.

Taxon	Mean density ($N \cdot 10m^{-2}$)							
	Baseline				Summer 1992			
	$Rank_B$	D_{BR}	D_{PR}	D_{both}	$Rank_A$	D_{BR}	D_{PR}	D_{both}
Priacanthus spp(PL)	10	.02	.85	.48	86	<.01	abs	<.01
Neoniphon sammara(PL)	11	.04	.52	.31	10	abs	.59	.30
Stethojulis balteata(BC)	12	.15	.40	.29	16	.04	.25	.16
Acanthurus triostegus(HERB)	**13**	**.13**	**.39**	**.28**	**8**	**.33**	**.75**	**.56**
Centropyge potteri(HERB)	**14**	**.17**	**.35**	**.27**	**12**	**.08**	**.36**	**.23**
Labroides phthirophagus(BC)	15	.04	.35	.21	15	<.01	.35	.20
Canthigaster jactator(BC)	16	.12	.26	.20	14	.12	.30	.22
Chromis hanui(PL)	17	.27	.12	.19	19	.07	.21	.15
Chromis vanderbilti(PL)	18	.32	abs	.16	7	1.26	abs	.63
Pervagor spilosoma(CO)	19	.01	.26	.15	79	<.01	abs	<.01
Acanthurus nigroris(HERB)	**20**	**.25**	**.02**	**.12**	**as surgeonfish pooled abs**	**.11**	**abs**	**.06**

Table 4.--Continued.

Taxon	Mean density ($N \cdot 10m^{-2}$)							
	Baseline				Summer 1992			
	$Rank_B$	D_{BR}	D_{FR}	D_{both}	$Rank_A$	D_{BR}	D_{FR}	D_{both}
Mulloidichthys flavolineatus(BC)	28	.18	.02	.09	9	abs	.84	.42
Zebrasoma flavescens(HERB)	**45**	**.02**	**.04**	**.03**	**11**	**abs**	**.45**	**.26**
Thalassoma ballieui(BC)	31	.14	.04	.08	17	.12	.18	.15
Parupeneus multi-fasciatus(BC)	29	.04	.12	.09	18	.04	.23	.15
Bodianus bilunulatus(BC)	30	.06	.10	.08	20	.06	.15	.11
Top 20 fishes		7.46	16.36	12.4		3.91	16.28	10.8
Total fishes		9.06	17.97	14.4		4.07	18.54	12.1

Table 5.--Summary of nominal "Before-After" changes in density ($N \cdot 10m^{-2}$) for the "Top 30" taxa of reef fishes observed at French Frigate Shoals, Northwestern Hawaiian Islands. Taxa are classified by major trophic level and by feeding guild within the carnivore level. Numbers in parentheses indicate the number of taxa that significantly decreased out of the total number tested in the particular trophic level or guild. Also summarized are results of the binomial test, using an alpha-level adjusted for the multiple comparison.

	Number of "Top 30" Taxa	
	Increasing	Decreasing
Herbivores	3	3
Secondary consumers	7	17
benthic carnivores	6	8(1[a])
zooplanktivores	1	6(2[a])
corallivores	0	2(1[a])
piscivores	0	1
Total	10	20

H_o : # decreases = # increases
H_a : # decreases > # increases

20/30 decreases; P=.05 (binomial test)

[a]Significant at P<.001, where $\alpha_{crit} = .05/30 = .002$

Table 6.--Summary of "Before-After" comparisons of densities ($N \cdot 10m^{-2}$) for major functional groupings of fishes at French Frigate Shoals, Northwestern Hawaiian Islands. Statistical conclusions are based on the results of parametric matched-pair (M-P) *t*-tests. Mean density data were matched by station and the grand mean of the signed differences (deltas) between sampling periods for all nine, barrier and patch reef stations tested against the null and 2-tailed alternative hypotheses, H_o: mean delta = 0 and H_a: mean delta ≠ 0. Each estimated mean and one standard error of the mean (SEM, in parentheses) are also provided for baseline samples.

Trophic level/guild	Baseline density ($N \cdot 10m^{-2}$) Mean (SE)	Pct of total	Apparent change (Pct)	M-P *t*-test *t*	P	Conclusion
Total fishes[a]	14.3 (2.0)	100	- 16	1.73	.12	ns
Herbivores	4.4 (0.6)	31	+ 10	0.66	.53	ns
Secondary consumers	9.9 (1.7)	69	- 27	2.28	.05	ns[b]
benthic carnivores	5.6 (0.8)	38	- 27	2.43	.04	ns[c]
planktivores	3.8 (1.1)	27	- 14	1.50	.17	ns
corallivores	0.35 (.07)	3	- 70	4.20	.003	SIG[c]
piscivores	0.14 (.04)	1	0	1.36	.21	ns

[a]Excluding sharks & jacks

[b]$\alpha_{crit} = \alpha_{.05}/2 = .025$

[c]$\alpha_{crit} = \alpha_{.05}/4 = .0125$

Table 7.--Summary of "Before-After" comparisons of relative (rank) densities for major functional groupings of fishes at French Frigate Shoals, Northwestern Hawaiian Islands. Statistical conclusions are based on results of nonparametric, Wilcoxon matched-pair signed-ranks (M-P S-R) tests. Density data were matched by station, and the signed differences (between sampling periods) ranked among the nine barrier and patch reef stations. The "T" statistic represents the sum of the smaller like-signed ranks (Siegel and Castellan 1988).

Trophic level/guild	M-P S-R Test		
	T	P	Conclusion
Total fishes[a]	9	>.10	ns
Herbivores	22	>>.10	ns
Secondary consumers	7	>.05	ns[b]
benthic carnivores	8	.10	ns[c]
planktivores	19	>>.10	ns
corallivores	0	.02	~SIG[c]
piscivores	12	>.10	ns

[a]Excluding sharks & jacks

[b]$\alpha_{crit} = \alpha_{.05}/2 = .025$

[c]$\alpha_{crit} = \alpha_{.05}/4 = .0125$

Table 8.--Summary results of tests to estimate the statistical power (1 minus Type II error), at α_2=.05 and at α_2=.10, using paired *t*-tests of "before minus after" deltas of mean density data for major functional groupings of fishes at French Frigate Shoals, Northwestern Hawaiian Islands. Also estimated are the sample sizes (number of stations sampled four times each in "before" and "after" periods) necessary to detect a 50% change in density with a power of 0.80.

Variable	Observed change (pct)	Power to detect 50% change at α_2=.05	Power to detect 50% change at α_2=.10	*N* needed[a] to detect 50% change at α_2=.05	*N* needed[a] to detect 50% change at α_2=.10
Total fishes	-16	.21	.33	12	9
Herbivores	+10	.10	.18	15	11
Secondary consumers	- 27	.32	.47	15	11
Benthic carnivores	- 27	.36	.51	13	10
Zooplanktivores	- 14	.16	.27	> 100	
Corallivores	- 70	.79	.89	30	23

[a]Power = .80

Appendix Table 1.--List of sampling dates and station specifics for baseline (1980-83) and July 1992 fish sampling at French Frigate Shoals, Northwestern Hawaiian Islands. Only the 'JDP' survey type was used in the analyses. Reef types are designated 'BR' for "barrier reef" and 'PR' for "patch reef", and sampling periods as 'PRE_' for "Before" and 'POST' for "After". "Nmbr taxa" refers to the number of species or subfamily-level taxa recognized on the transect. "Area" is the planar reef area used to standardize fish counts to density.

Date	Survey type	Reef type	Period	Station	Transect	Nmbr taxa	Area (m^2)
30MAY80	JDP	BR	PRE_	4	1	26	250
31MAY80	JDP	BR	PRE_	4	2	28	250
03NOV80	JDP	BR	PRE_	4	3	35	500
03NOV80	JDP	BR	PRE_	4	4	32	500
30OCT80	JDP	PR	PRE_	5c	1	35	150
30OCT80	JDP	PR	PRE_	5c	2	33	150
18MAR83	JDP	PR	PRE_	5c	3	34	100
19MAR83	JDP	PR	PRE_	5c	4	25	150
21MAY80	JDP	PR	PRE_	5d	1	28	150
22MAY80	JDP	PR	PRE_	5d	2	26	150
29OCT80	JDP	PR	PRE_	5d	3	35	150
29OCT80	JDP	PR	PRE_	5d	4	38	150
18MAR83	JDP	PR	PRE_	5d	5	36	200
19MAR83	JDP	PR	PRE_	5d	6	37	150
22MAY80	JDP	PR	PRE_	5e	1	35	150
22MAY80	JDP	PR	PRE_	5e	2	35	150
30OCT80	JDP	PR	PRE_	5e	3	33	150
30OCT80	JDP	PR	PRE_	5e	4	33	150
19MAR83	JDP	PR	PRE_	5e	5	37	150
19MAR83	JDP	PR	PRE_	5e	6	36	150
24MAR83	JDP	PR	PRE_	5e	7	29	150
21MAY80	JDP	PR	PRE_	5f	1	26	150
21MAY80	JDP	PR	PRE_	5f	2	33	150
30MAY80	JDP	PR	PRE_	5f	3	18	150
25MAY80	JDP	BR	PRE_	6	1	18	250
26MAY80	JDP	BR	PRE_	6	2	36	250
26MAY80	JDP	BR	PRE_	6	3	35	500
01NOV80	JDP	BR	PRE_	6	4	24	500
01NOV80	JDP	BR	PRE_	6	5	33	500
28MAY80	JDP	BR	PRE_	7	1	38	450
28MAY80	JDP	BR	PRE_	7	2	39	450
31OCT80	JDP	BR	PRE_	7	3	37	350
31OCT80	JDP	BR	PRE_	7	4	37	350
02JUN80	JDP	BR	PRE_	8	1	35	250
03JUN80	JDP	BR	PRE_	8	2	33	250

Appendix Table 1.--Continued.

Date	Survey type	Reef type	Period	Station	Transect	Nmbr taxa	Area (m^2)
08NOV80	JDP	BR	PRE_	8	3	50	500
11NOV80	JDP	BR	PRE_	8	4	44	500
23MAR83	JDP	PR	PRE_	23	1	31	100
23MAR83	JDP	PR	PRE_	23	2	27	100
23MAR83	JDP	PR	PRE_	23	3	31	100
25MAR83	JDP	PR	PRE_	23	4	31	100
25MAR83	JDP	PR	PRE_	23	5	29	100
26MAR83	JDP	PR	PRE_	23	6	30	100
11JUL92	JDP	BR	POST	4	1	19	500
11JUL92	JDP	BR	POST	4	2	22	500
11JUL92	JDP	BR	POST	4	3	16	500
11JUL92	JDP	BR	POST	4	4	20	500
08JUL92	JDP	PR	POST	5c	1	23	150
08JUL92	JDP	PR	POST	5c	2	28	150
08JUL92	JDP	PR	POST	5c	3	27	150
08JUL92	JDP	PR	POST	5c	4	25	150
10JUL92	JDP	PR	POST	5d	1	31	150
10JUL92	JDP	PR	POST	5d	2	30	150
10JUL92	JDP	PR	POST	5d	3	29	150
10JUL92	JDP	PR	POST	5d	4	32	150
10JUL92	JDP	PR	POST	5e	1	27	150
10JUL92	JDP	PR	POST	5e	2	24	150
10JUL92	JDP	PR	POST	5e	3	30	150
10JUL92	JDP	PR	POST	5e	4	28	150
09JUL92	JDP	PR	POST	5f	1	27	150
09JUL92	JDP	PR	POST	5f	2	29	150
09JUL92	JDP	PR	POST	5f	3	31	150
09JUL92	JDP	PR	POST	5f	4	35	150
12JUL92	JDP	BR	POST	6	1	26	500
12JUL92	JDP	BR	POST	6	2	23	500
12JUL92	JDP	BR	POST	6	3	26	500
12JUL92	JDP	BR	POST	6	4	21	500
07JUL92	JDP	BR	POST	7	1	27	500
07JUL92	JDP	BR	POST	7	2	24	500
07JUL92	JDP	BR	POST	7	3	27	500
07JUL92	JDP	BR	POST	7	4	26	500
08JUL92	JDP	BR	POST	8	1	20	500
08JUL92	JDP	BR	POST	8	2	27	500
08JUL92	JDP	BR	POST	8	3	26	500
08JUL92	JDP	BR	POST	8	4	20	500
09JUL92	JDP	PR	POST	23	1	29	150
09JUL92	JDP	PR	POST	23	2	30	150
09JUL92	JDP	PR	POST	23	3	27	150
09JUL92	JDP	PR	POST	23	4	28	150
04JUL92	EED	BR	POST	4	1	36	300

Appendix Table 1.--Continued.

Date	Survey type	Reef type	Period	Station	Transect	Nmbr taxa	Area (m^2)
04JUL92	EED	BR	POST	4	2	18	300
04JUL92	EED	BR	POST	4	3	24	300
07JUL92	EED	BR	POST	4	4	20	300
05JUL92	EED	PR	POST	5c	1	26	60
05JUL92	EED	PR	POST	5c	2	28	60
14JUL92	EED	PR	POST	5c	3	26	90
14JUL92	EED	PR	POST	5c	4	30	90
06JUL92	EED	PR	POST	5d	1	30	60
06JUL92	EED	PR	POST	5d	2	31	60
07JUL92	EED	PR	POST	5d	3	24	60
07JUL92	EED	PR	POST	5d	4	28	60
04JUL92	EED	PR	POST	5e	1	28	120
04JUL92	EED	PR	POST	5e	2	25	120
12JUL92	EED	PR	POST	5e	3	26	180
13JUL92	EED	PR	POST	5e	4	27	90
06JUL92	EED	PR	POST	5f	1	29	60
06JUL92	EED	PR	POST	5f	2	27	60
14JUL92	EED	PR	POST	5f	3	31	90
14JUL92	EED	PR	POST	5f	4	30	90
05JUL92	EED	BR	POST	6	1	29	300
05JUL92	EED	BR	POST	6	2	34	300
12JUL92	EED	BR	POST	6	3	20	300
12JUL92	EED	BR	POST	6	4	13	300
06JUL92	EED	BR	POST	7	1	27	300
06JUL92	EED	BR	POST	7	2	37	300
12JUL92	EED	BR	POST	7	3	33	300
12JUL92	EED	BR	POST	7	4	21	300
05JUL92	EED	BR	POST	8	1	19	300
05JUL92	EED	BR	POST	8	2	23	300
11JUL92	EED	BR	POST	8	3	22	300
11JUL92	EED	BR	POST	8	4	23	300
04JUL92	EED	PR	POST	23	1	32	120
04JUL92	EED	PR	POST	23	2	23	120
13JUL92	EED	PR	POST	23	3	23	90
13JUL92	EED	PR	POST	23	4	26	90

Appendix Table 2.--List of all fishes (species and higher taxa within family) encountered on transects and free-swims (length estimation task, July 1992 only) at French Frigate Shoals during 1980/83 baseline ('PRE_') surveys and the July 1992 ('POST') survey. Presence = 'x'; 'N/R' = "not recorded"; 'JDP' and 'EED' refer to survey types; 'JDP' survey type only used in analyses. "IDNO" designates 4-digit computer code. The multiple records for each survey type in the 'POST' period refer to Divers 1, 2, and 3.

		'PRE_'	'POST'						
FAMILY/taxon	IDNO	'JDP'	'JDP'			'EED'			
CARCHARHINIDAE	100	N/R	x	x		x	x	x	
carcharhinid sp	101			x		x	x	x	
Carcharhinus amblyrhynchos	102		x				x	x	
Galeocerdo cuvier	103		x						
Triaenodon obesus	104		x	x					
CARANGIDAE	200	x	x	x	x	x	x	x	
Caranx ignobilis	201	x	x	x	x	x	x	x	
Caranx melampygus	202	x	x	x	x	x	x	x	
Decapterus macarellus	203	x	--	not recorded --					
MURAENIDAE	300	x	x	x	x			x	x
Gymnothorax flavimarginatus	301	x		x					x
Gymnothorax spp	302	x	x	x	x			x	
Gymnothorax undulatus	303	x						x	
Gymnothorax eurostus	304	x							
AULOSTOMIDAE	400	x	x	x	x	x	x	x	x
Aulostomus chinensis	401	x	x	x	x	x	x	x	x
FISTULARIDAE	500	x				x			
Fistularia commersonii	501	x				x			
LUTJANIDAE	600	x	x	x	x			x	
Aprion virescens	602	N/R	x					x	
Lutjanus kasmira	603	x	x	x	x				
SYNODONTIDAE	700	x	x	x	x	x	x	x	x
Synodus spp	701	x	x	x	x	x	x	x	x
Saurida gracilis	702	x							
Saurida sp	703	x							
Synodus ulae	704	x							
HOLOCENTRIDAE	800	x	x	x	x	x	x	x	x
Adioryx spp	801	x	x	x	x	x	x	x	x
Neoniphon sammara	802	x	x	x	x	x	x	x	x
Myripristis spp	803	x	x		x	x	x	x	x
Sargocentron sp (= *Adioryx diadema*)	804	x				x			

Appendix Table 2.--Continued.

FAMILY/taxon	IDNO	'PRE_' 'JDP'	'POST' 'JDP'			'POST' 'EED'		
Sargocentron tiere (= *Adioryx tiere*)	805	x	x	x	x	x	x	x
Adioryx diadema	806	x						
Adioryx xantherythrum	808	x						
APOGONIDAE	900	x	x			x		
Apogon spp	901	x	x			x		
Apogon kallopterus	902	x						
Apogon maculiferus	903	x						
LETHRINIDAE	1000	x				x	x	
Monotaxis grandoculis	1001	x				x	x	
MULLIDAE	1100	x	x	x	x	x	x	x
Mulloidichthys sp	1101							x
Mulloidichthys flavo-lineatus	1102	x	x	x	x	x	x	x
Mulloidichthys vanico-lensis	1103	x	x	x	x	x	x	x
Parupeneus bifasciatus	1104	x					x	
Parupeneus chryserydros	1105	x	x	x	x		x	x
Parupeneus cyclo-stomus(=chryserydros)	1106	x	x			x	x	
Parupeneus multifasciatus	1107	x	x	x	x	x	x	x
Parupeneus pleurostigma	1108	x	x	x	x	x	x	x
Parupeneus porphyreus	1109	x	x	x		x	x	x
Parupeneus spp	1110		x					
LABRIDAE	1200	x	x	x	x	x	x	x
Anampses chrysocephalus	1201	x				x		
Anampses cuvier	1202	x	x	x	x	x	x	x
Bodianus bilunulatus	1203	x	x	x	x	x	x	x
Cheilinus unifasciatus	1204	x	x	x	x	x	x	x
Coris flavovittata	1205	x	x	x	x	x	x	x
Coris gaimard	1206	x	x			x		x
Coris spp	1207				x		x	x
Coris venusta	1208	x	x			x		
Epibulus insidiator	1209	x	x	x	x	x	x	x
Gomphosus varius	1210	x	x	x	x	x	x	x
Halichoeres spp	1211	x		x			x	
Labrid sp	1212						x	
Labroides phthirophagus	1213	x	x	x	x	x	x	x
Labroides sp	1214				x			x
Macropharyngodon sp	1215	x	x	x		x	x	
Novaculichthys taeniourus	1216	x			x	x		
Pseudocheilinus spp	1217	x	x	x	x	x	x	x
Stethojulis balteata	1218	x	x	x	x	x	x	x

Appendix Table 2.--Continued.

FAMILY/taxon	IDNO	'PRE_'	'POST'					
		'JDP'	'JDP'			'EED'		
Thalassoma ballieui	1219	x	x	x	x	x	x	x
Thalassoma duperrey	1220	x	x	x	x	x	x	x
Halichoeres ornatissimus	1221	x						
Pseudocheilinus octotaenia	1222	x						
Macropharyngodon geoffroy	1223	x						
Pseudojuloides cerasinus	1224	x						
Pseudocheilinus tetrataenia	1225	x						
Pseudocheilinus evanidus	1226	x						
Cheilinus bimaculatus	1227	x						
CIRRHITIDAE	1300	x	x	x	x	x	x	x
Cirrhitops fasciatus	1301	x	x		x	x		x
Cirrhitops sp	1302							x
Paracirrhites arcatus	1303	x	x	x	x	x	x	x
Paracirrhites forsteri	1304	x		x				x
Cirrhitus pinnulatus	1305	x	-- not recorded --					
SCORPAENIDAE	1400	x		x	x	x		x
Dendrochirus barberi	1401	x						x
Pterois sphex	1402	N/R			x			
Pterois spp	1403				x			
Taenianotus triacanthus	1404	x		x				x
Sebastapistes ballieui	1405	x	-- not recorded --					
PRIACANTHIDAE	1500	x	x			x		
Priacanthus spp	1501	x	x			x		
CHEILODACTYLIDAE	1600					x		
Cheilodactylus vittatus	1601	N/R				x		
BALISTIDAE	1700	x	x	x	x	x	x	x
Melichthys niger	1701	x			x	x	x	x
Melichthys vidua	1702	x	x		x	x	x	x
Rhinecanthus sp	1703							x
Sufflamen bursa	1704	x	x	x	x	x	x	x
Rhinecanthus rectangulus	1705	x						
CANTHIGASTERIDAE	1800	x	x	x	x	x	x	x
Canthigaster jactator	1801	x	x	x	x	x	x	x
OSTRACIIDAE	1900	x	x	x				
Ostracion meleagris	1901	x	x	x				
Lactoria fornasini	1902	x	-- not recorded --					
MONACANTHIDAE	2000	x	x	x	x		x	
Cantherhines spp	2001	N/R	x					
Pervagor spilosoma	2002	x	x	x	x		x	
POMACANTHIDAE	2100	x	x	x	x	x	x	x
Centropyge potteri	2101	x	x	x	x	x	x	x
CHAETODONTIDAE	2200	x	x	x	x	x	x	x
Chaetodon auriga	2201	x			x	x	x	x

Appendix Table 2.--Continued.

FAMILY/taxon	IDNO	'PRE_' 'JDP'	'POST' 'JDP'			'POST' 'EED'		
Chaetodon fremblii	2202	x	x	x	x	x	x	x
Chaetodon miliaris	2203	x	x	x	x	x	x	x
Chaetodon multicinctus	2204	x	x	x	x	x	x	x
Chaetodon ornatissimus	2205	x		x	x	x	x	x
Chaetodon quadrimaculatus	2206	x				x		
Chaetodon sp	2207		x	x	x			x
Chaetodon trifascialis	2208	N/R		x				
Chaetodon trifasciatus	2209	x	x	x	x	x	x	x
Chaetodon unimaculatus	2210	x	-- not recorded --					
Forcipiger flavissimus	2211	x	x	x	x	x	x	x
Chaetodon lunula	2212	x	-- not recorded --					
BLENNIIDAE	2300	x		x	x		x	
blenniid spp	2301	x		x	x		x	
Cirripectes spp	2302	x					x	
Cirripectes variolosus	2303	x		x				
Exallias brevis	2304	x	-- not recorded --					
POMACENTRIDAE	2400	x	x	x	x	x	x	x
Chromis hanui	2402	x	x	x	x	x	x	x
Chromis ovalis	2403	x	x	x	x	x	x	x
Chromis vanderbilti	2404	x	x	x	x	x	x	x
Dascyllus albisella	2406	x	x	x	x	x	x	x
Plectroglyphidodon imparipennis	2407	x	x	x	x	x		
Plectroglyphidodon johnstonianus	2408	x	x	x	x	x	x	x
pomacentrid sp	2409							x
Stegastes fasciolatus	2410	x	x	x	x	x	x	x
Chromis verater	2411	x	-- not recorded --					
KYPHOSIDAE	2500	x	x	x	x	x	x	x
Kyphosus cinerascens	2501	x	x	x	x	x	x	x
SCARIDAE	2600	x	x	x	x	x	x	x
Scarus lauia(=dubius)	2601	x	x			x		
Scarus perspicillatus	2602	x	x	x	x	x	x	x
Scarus sordidus	2603	x	x	x		x	x	x
Scarus spp	2604				x			x
scarid spp juvenile	2605	x	x	x	x	x	x	x
Calotomus sp	2607	x	-- not recorded --					
ACANTHURIDAE	2700	x	x	x	x	x	x	x
Acanthurus spp	2701		x		x		x	
Acanthurus achilles	2702	x	x	x	x	x	x	x
Acanthurus blochii	2703	N/R		x	x	x	x	x
Acanthurus mata(=blochii)	2704	N/R				x		
Acanthurus nigrofuscus	2705	x		x	x	x	x	x
Acanthurus nigroris	2706	x		x		x	x	x
Acanthurus olivaceus	2707	x	x	x	x	x	x	x

Appendix Table 2.--Continued.

FAMILY/taxon	IDNO	'PRE_' 'JDP'	'POST' 'JDP'			'POST' 'EED'		
Acanthurus triostegus	2708	x	x	x	x	x	x	x
Acanthurus xanthopterus	2709	N/R	x	x	x	x		x
Ctenochaetus strigosus	2710	x	x	x	x	x	x	x
Naso lituratus	2711	x	x	x	x	x	x	x
Naso unicornis	2712	x	x	x	x	x	x	x
Zebrasoma flavescens	2713	x	x	x	x	x	x	x
Acanthurus dussumieri	2714	x	-- not recorded --					
ZANCLIDAE	2800	x	x	x	x	x	x	x
Zanclus cornutus	2801	x	x	x	x	x	x	x
DIODONTIDAE	2900	x	-- not recorded --					
Diodon holocanthus	2901	x						
BELONIIDAE	3000	x	-- not recorded --					
"needlefish"	3001	x						
TETRAODONTIDAE	3100	x	-- not recorded --					
Arothron meleagris	3101	x						

Appendix Table 3.--Estimated percentage cover of the green alga, *Microdictyon* sp, at reef fish sampling stations, French Frigate Shoals, Northwestern Hawaiian Islands. Cover estimates are semi-quantitative--based on baseline station descriptions and digitized estimates of algal cover using videotapes of station habitat recorded on the summer 1992 survey.

Reef type	Station	Area searched (m^2)	% cover	
			1980-83	1992
BR	4	500	0	4.5
PR	5c	72	no data	29.5
PR	5d	127	0	27.0
PR	5e	127	0	27.9
PR	5f	127	0	27.5
BR	6	500	0	0
BR	7	500	no data	0
BR	8	500	0	9.6
PR	23	-	no data	no data

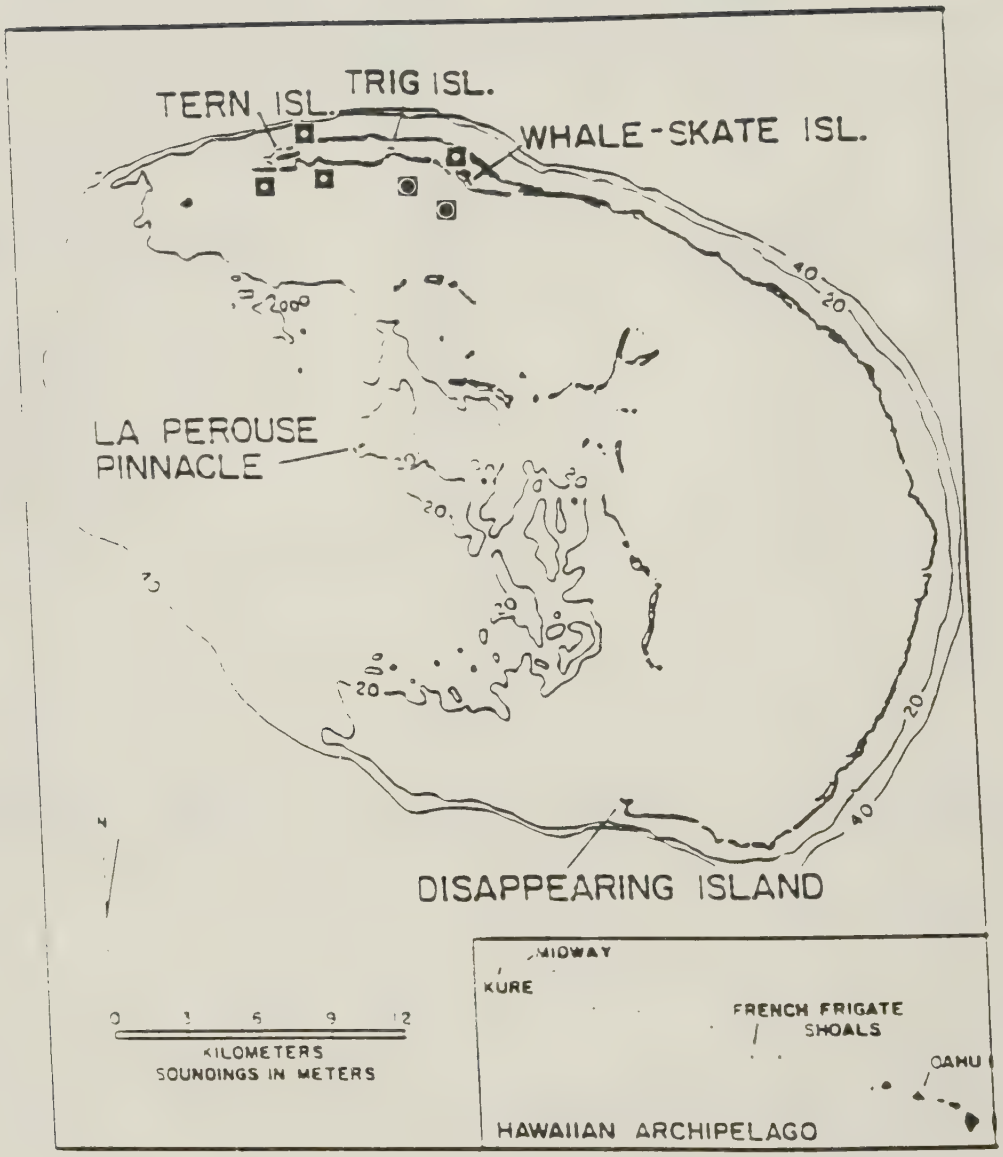

Figure 1.--Chart of French Frigate Shoals (FFS), Northwestern Hawaiian Islands, showing the locations of the barrier reef (□) and patch reef (◙) stations at which reef fishes were sampled in 1980-83 and 1992. The four patch reefs comprising stations 5c, d, e, and f are indicated by a single symbol just southeast of Trig Island.

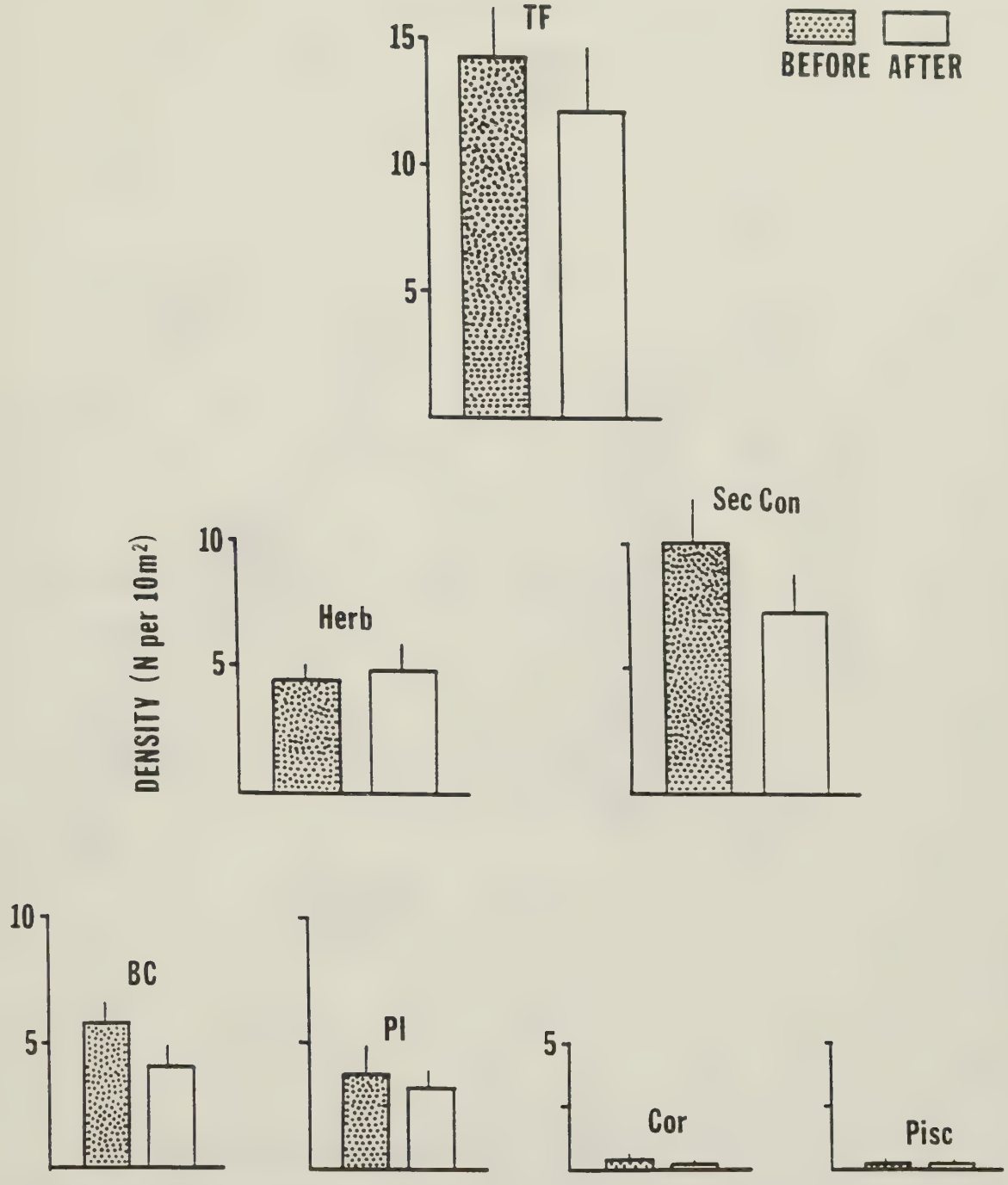

Figure 2.--Histograms of numerical densities ($N \cdot 10m^{-2}$) for total fishes (TF; top); two major trophic levels (Herbivores = Herb; Carnivores or Secondary Consumers = Sec Con; middle); and four carnivore guilds (Benthic Carnivores = BC; Zooplanktivores = PL; Corallivores = COR; and Piscivores = PISC; bottom) of reef fishes at FFS during "Before" (1980/1983) and "After" (1992) sampling periods. Data are unweighted grand means for the two (barrier and patch reef) habitat types. One standard error (SEM) of each mean estimate is provided.

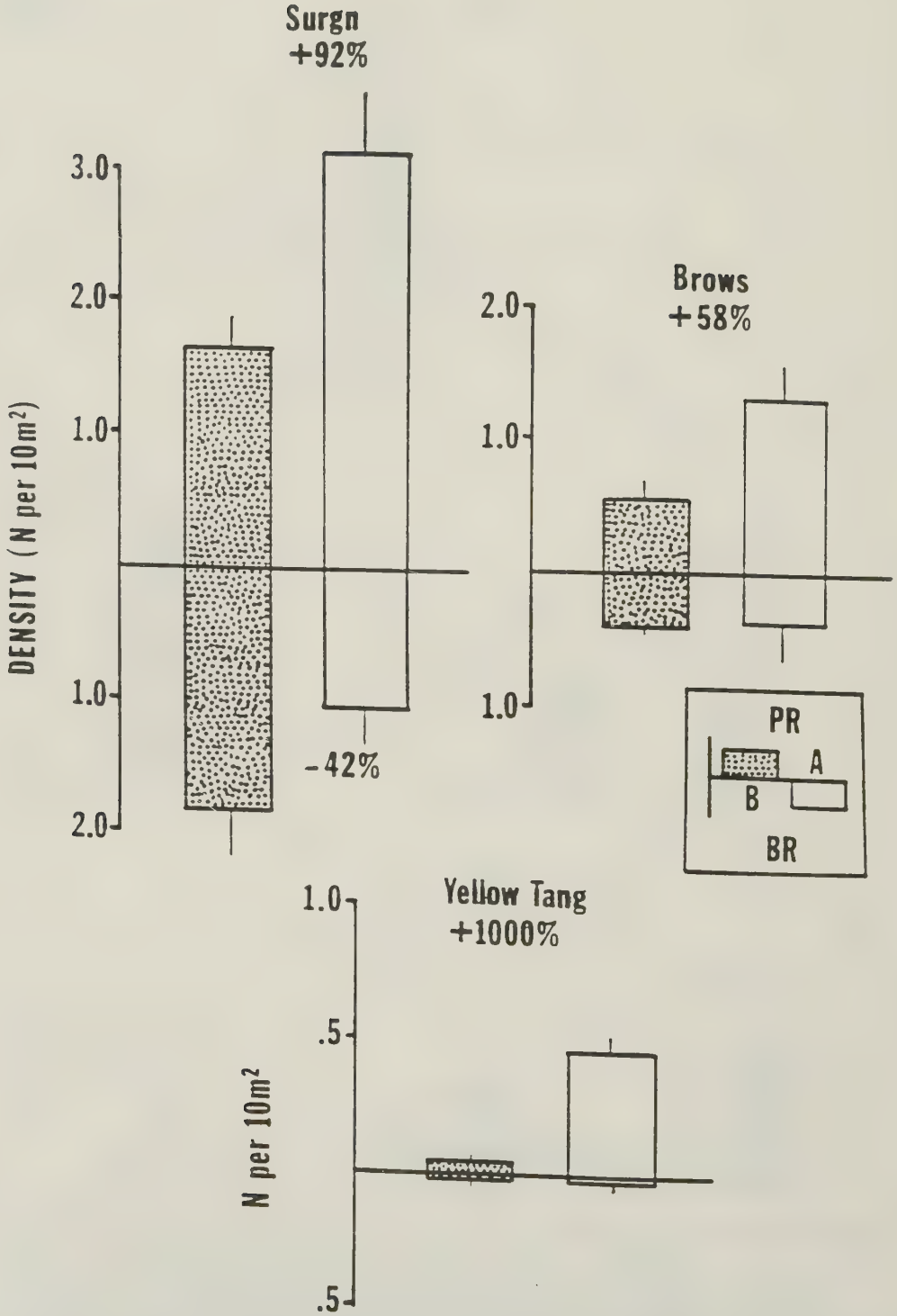

Figure 3.--Histograms of numerical densities ($N \cdot 10m^{-2}$) on barrier (BR) and patch reefs (PR) for (A) all surgeonfishes (Surgn) of the family Acanthuridae, (B) the guild of surgeonfishes that are browsers (Brows; Jones 1968) of filamentous benthic algae, and (C) for yellow tang, *Zebrasoma flavescens*, a major species of the browser guild on patch reefs. One standard error (SEM) of each mean estimate is provided.

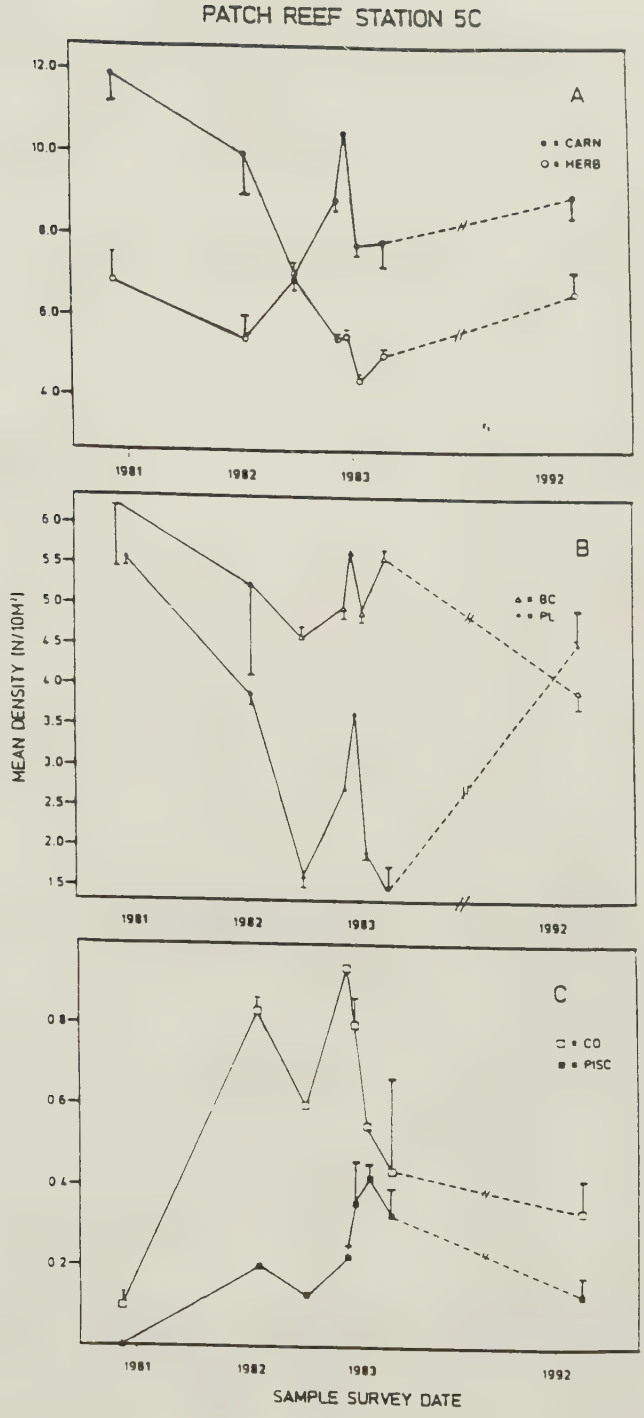

Figure 4.--Trend plots of the estimated mean numerical densities ($N \cdot 10\ m^{-2}$) for (A) Primary Consumers (Herb) and Secondary Consumers (Sec Con), (B) Benthic Carnivores (BC) and Zooplanktivores (PL), and (C) Corallivores (COR) and Piscivores (PISC), at FFS patch reef station 5c on each of eight surveys during October 1980-July 1992, inclusive. One "standard error" of each survey mean (SEM) is noted; these SEMs are undoubtedly biased low because the repeat counts upon which they are based are not independent replicates.

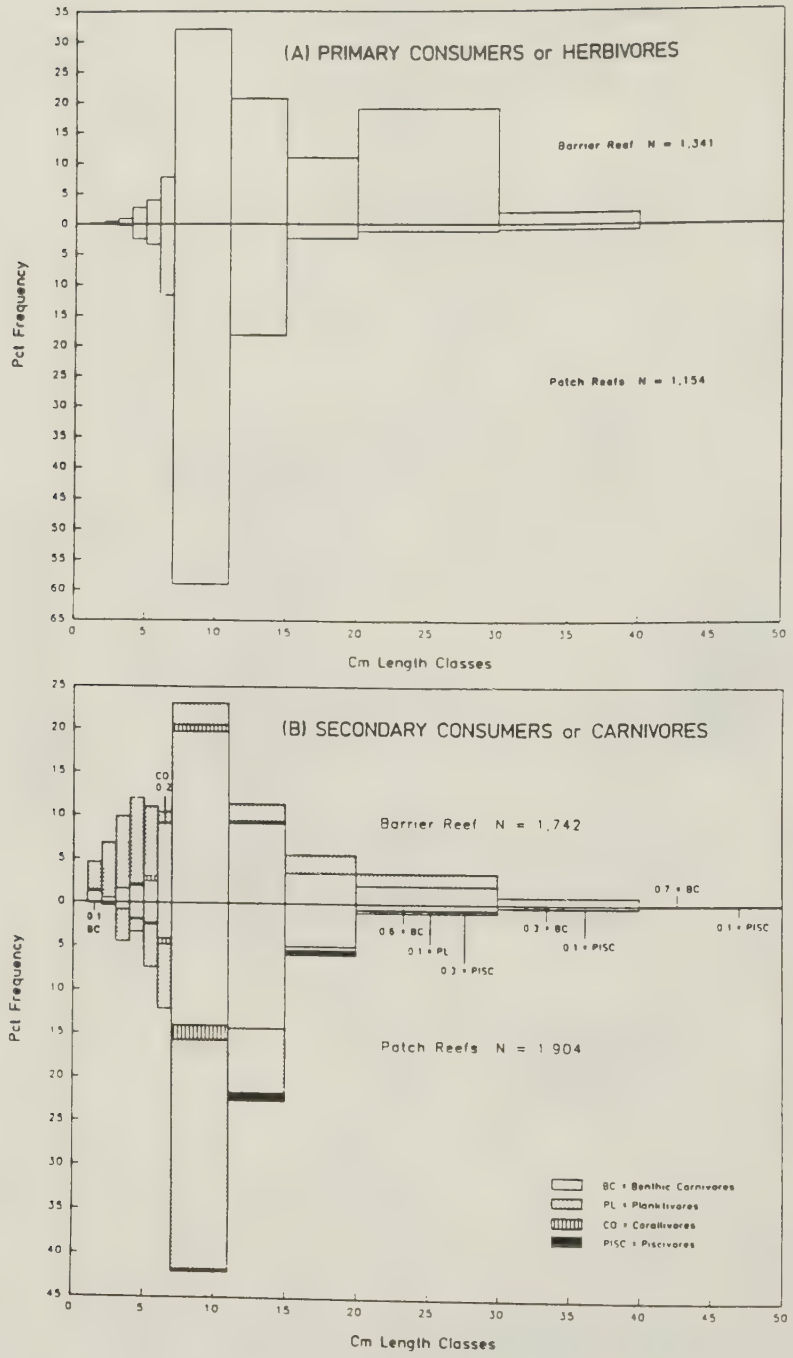

Figure 5.--Histograms of percentage frequency distributions of body length classes (cm SL) for (A) Primary Consumers or Herbivores and (B) Secondary Consumers or Carnivores. In each (A, B) panel, distributions are plotted for barrier reef stations and for patch reef stations above and below the horizontal axis, respectively. Within panel (B), Carnivore distributions are partitioned into Benthic Carnivore (BC), Zooplanktivore (PL), Corallivore (COR), and Piscivore (PISC) guilds.

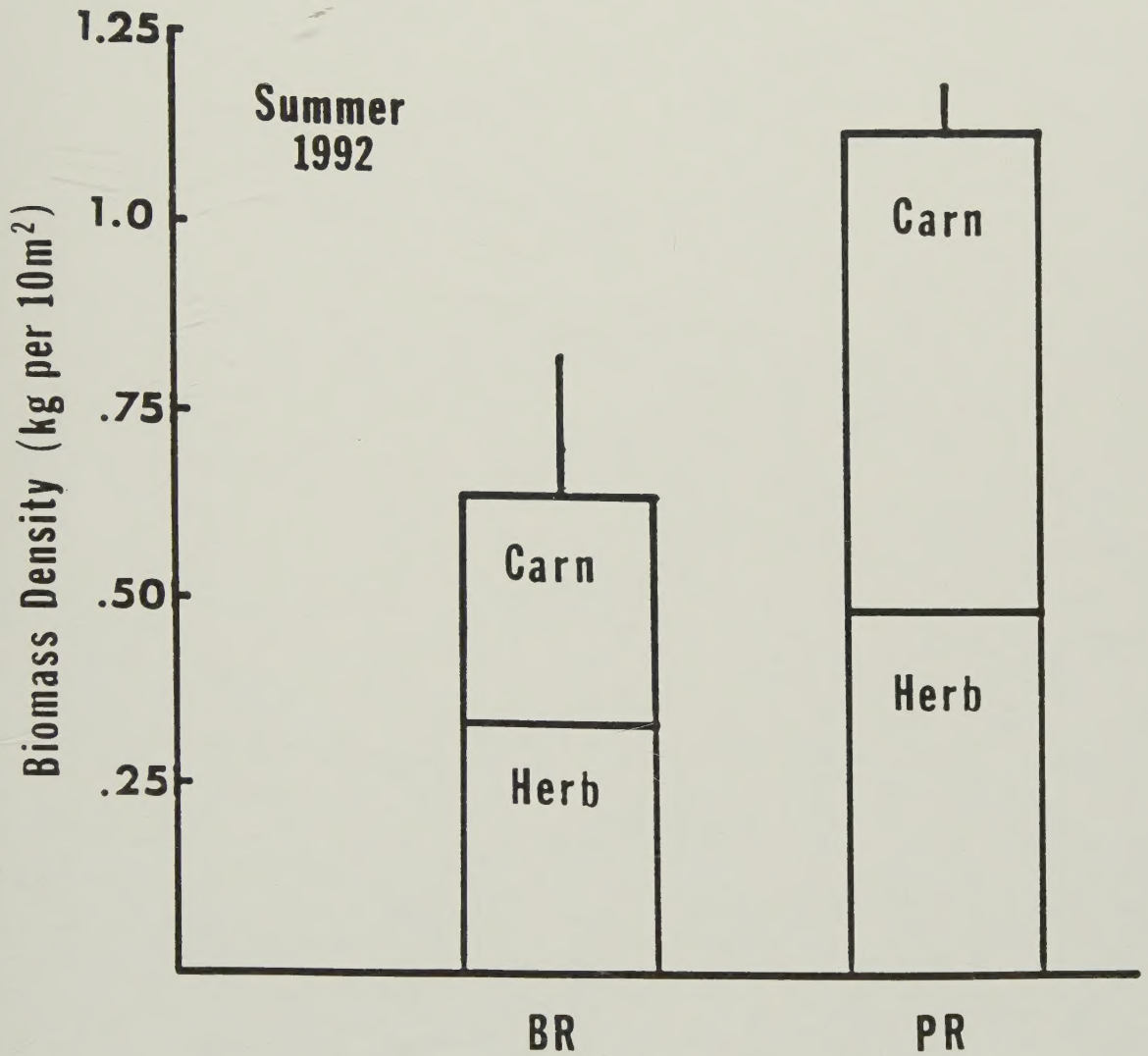

Figure 6.--Histograms of estimated mean biomass densities of herbivorous (Herb) and carnivorous (Carn) fishes on barrier (BR) and patch reefs (PR) at FFS during summer 1992. Also indicated is one standard error (SEM) of the estimated biomass density for total (herbivorous plus carnivorous) fishes in each habitat.